COMMENTARY

Introduced species shape insular mutualistic networks

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Our planet's biosphere, comprising all living beings and their interactions, is experiencing unprecedented changes. Within a few decades, we could face entirely new climates, and radically altered species compositions and distributions, forming novel networks of biotic interactions. To date, however, most studies have focused on ecosystems under low levels of invasion and turnover. As novel networks are expected to function differently with the level of invasion and turnover, we have yet to see whether the loss of an entire functional guild from an ecological interaction network can be supplanted by introduced species alone. This work (1) provides a step into unchartered waters through investigating species' roles in a highly invaded novel ecosystem. The volcanic island of O'ahu in the Hawaiian archipelago is inhabited by one million residents and is frequented by many tourists each year. It is also the newfound home for many introduced species. According to this 3-y study of nearly 3,500 fecal samples and 5,000 camera trapping images over seven sites (1), the seed dispersal network on O'ahu has been found to be taken over entirely by novel interactions between introduced birds and introduced plants, amounting to 93% of all observed events, with the rest also comprising novel interactions between introduced and native species (Fig. 1)—with no interactions being found between native birds and native plants. Species assemblages on O'ahu were also found to be composed predominately of introduced species (Fig. 1). It is evident that the entire function of seed dispersal by frugivorous birds in this insular ecosystem has been taken over by introduced species, with the red-billed leiothrix, *Leiothrix lutea*, and the pigeonberry *Rivina humilis* serving as network hubs. This calls for a genuine dialogue on how to manage such novel ecosystems (2) and guide the public perception on ecological novelty from biological invasions and anticipated species extinctions in this era of Anthropocene (3).

The dominance of introduced species in highly invaded insular ecosystems of O'ahu supports, indirectly,

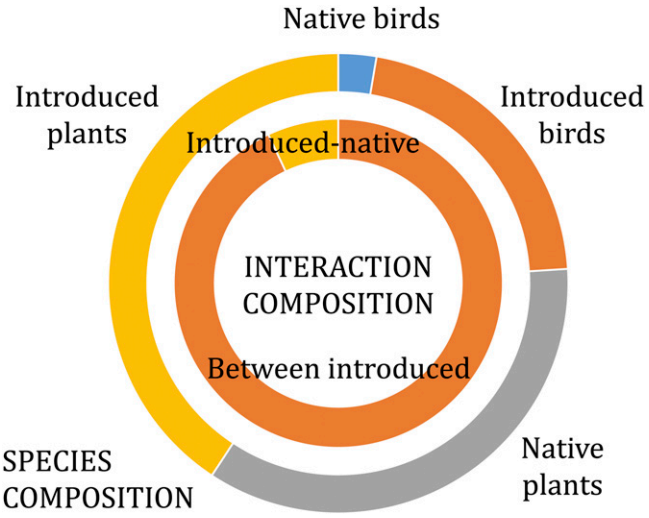

Fig. 1. Species composition (outer circle) and interaction composition (inner circle) of seed dispersal networks on O'ahu of Hawai'i. Of the 18 species recorded, 16 are introduced; of the 57 plant species, 31 are introduced. All observed interactions are novel, between introduced species (93%), and between introduced and native species (7%). See ref. 1 for detail.

the means of ecological fitting in establishing novel biotic interactions between species sharing little evolutionary history (4). Indeed, with certain levels of trait complementary, such as between the gap size of frugivorous birds and the fruit size (1), interaction rewiring and switching are sufficient to explain the establishment of such novel interactions. As a result from ecological fitting, the observed interaction strength between two species reflects both the encounter rate (considered as a neutral force) and their trait complementarity (often described as an interaction kernel function; dubbed a niche-based force) (1). It is, therefore, possible to predict the structure of a seed dispersal network from the heterogeneous fleshy fruit resources in the landscape (5). It also means that we can use the trait dispersion of residing species to

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assess the invasibility of an ecological network and the invasiveness of prospective nonnative species (6). This allows invasion science to move away from its traditional, often contentious, species-centric view to embrace the trait paradigm in community ecology. Multiple hypotheses exist to elaborate the effect of ecological fitting and interaction rewiring on invasion success. In particular, the missed mutualism hypothesis predicts that species benefitting from mutualistic interactions in their native range must establish a similar type of positive interaction in the introduced range for invasion while the new association hypothesis postulates that novel interactions between natives and nonnative species can interfere with the establishment of the nonnative species. Without the cointroduction of their mutualists, many specialized species failed to establish (7). Nevertheless, the excessively high proportion of novel interactions on O'ahu supports the hypothesis of invasional meltdown (8) that the novel interactions between introduced species facilitate further invasions in recipient ecosystems.

Seed dispersal interactions in an ecological network are asymmetric and directed; that is, species *j*'s interaction strength toward species *i* is not necessarily equal to species *i*'s interaction strength on species *j* ($a_{ij} \neq a_{ji}$ in the interaction matrix). This is because the benefit and cost (thus payoff) of each event differs for seed dispersers and fruiting plants. This asymmetric benefit and cost suggests that the two guilds are not committed at the same level and, as such, contribute to network structures and functions differently. Most bird species are not obligatory frugivores but rather omnivores, and their responses are expected to be more flexible than plants, consequently contributing more to the structure and stability of seed dispersal networks (1). However, this work (1) took the interactions as undirected, with the interaction strength between species *i* and *j* defined as the number of observed events. Although doing so clearly is due to data constraints, benefits and costs in seed dispersal events need to be quantified so that the payoff to involved species (the strength and the direction of interaction) can be quantified. This is especially needed for insular ecosystems as interaction asymmetry can be augmented in such ecosystems due to the loss of native frugivores (9).

According to the modern coexistence theory (10), the coexistence of species is primarily controlled by niche- and neutral-based processes, through achieving niche separation and fitness equivalence between directly interacting species. As a species' abundance is a key predictor of its role in ecological networks (1), it is foreseeable that there should be different interplays of niche and neutral processes in driving the distributions and interactions of abundant versus rare species (11). Furthermore, ecological networks also harbor complex interaction chains that often involve many species, which can greatly affect species coexistence and invasion. Such network structures can profoundly affect network stability and species coexistence. For instance, instead of the interaction hierarchy between species, multiple species in an ecological network can form intransitive interactions and feedback loops (12), posing as a third mechanism of community stability and species coexistence. For instance, introduced species that can foster intransitive loops in the recipient ecosystems, either directly or indirectly, can increase its chance and impact of invasion (13). Consequently, not only can neutral- and niche-based forces dictate species' roles, but also the network structure itself, such as connectance, nestedness, and modularity (1). A key research priority, therefore, is to go beyond merely dissecting network assembly according to niche- versus neutral-based processes, but explore interaction complexity (e.g., interaction loops) that is typical to network settings, to better our analyses of ecosystem functioning in invaded ecological networks.

A highly invaded ecological network is jammed by the constant flux of introduced species, exhibiting transient dynamics at marginal instability. Much like packing your suitcase before traveling, you need to rearrange and discard certain items to make space for additional items.

While the impacts of biological invasions on the abundance and diversity of the recipient ecosystems are obvious, the temporal assembly and turnover can play out in an invaded ecological network in many different ways.

The relationship between structural complexity and network stability has long been debated as the stability criterion (14). A resilient ecosystem holds its species together by satisfying its stability criterion, while biological invasions and subsequent species extinctions push ecological networks to the point of marginal instability, violating the stability criterion. An open adaptive network, therefore, operates at its marginal instability and loosens the complexity–stability relationship regardless of the emergent network structures. Importantly, lack of a strong complexity–stability relationship does not suggest that ecological networks are randomly structured. Rather, many realistic network structures emerge simultaneously while the entire network converges to marginal instability via coevolution and ecological fitting. Both empirical and theoretical works support the lack of strong complexity–stability relationships and trivial changes in network structures from biological invasions (15). It warrants attention that works do demonstrate drastic changes in network structures (1, 16, 17) when comparing network structures of alien species alone versus those only considering native resident species, while both are just a subset of the invaded ecological network. This marginal instability then allows for forecasting of the wax and wane of residing species in an invaded ecological network (18).

This study (1) adds to a wave of research that documents the role of biotic interactions in driving insular community assembly, which has been largely ignored in the classic theory of island biogeography (19). The classic theory clarifies how the rates of species inflow and outflow depend on the island area and isolation, and how the two rates jointly maintain the dynamic equilibrium of an insular biota. Although it highlights the constant transition and turnover of the species assemblage in any ecological communities, the role of biotic interactions between residing species was, nevertheless, downplayed in modifying the rates of extinctions and successful introductions. The network of biotic interactions can function as magnets to involved species and affect their demographic performance and invasion dynamics. By documenting the detailed interaction structures (1), it lays the foundation for long-term studies to elucidate how the rates of introduction and extinction are related to the architecture of ecological networks, to advance the classic theory of island biogeography. In particular, we need to acknowledge the nonequilibrial, dynamic nature of assembly and disassembly from biological invasions. While the impacts of biological invasions on the abundance and diversity of the recipient ecosystems are obvious, the temporal assembly and turnover can play out

in an invaded ecological network in many different ways. When exploring temporal turnover during insular assembly to support the classic theory of island biogeography, Diamond (20) ends with a prelude to invaded ecological networks: "Ecological consequences of these insular invasions, extinctions, and variations in species diversity include striking expansions and compressions of the niche of a given species, depending upon the competing species pool it faces."

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